

THE OIL GLAND OF BIRDS

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THE uropygial gland of birds, otherwise known as the oil gland, preen gland or rump gland has been the subject of much discussion and investigation for more than 100 years. The literature dealing with this subject is widely scattered in many journals and in many languages. The best review was written by Hou (1928b) in *The Chinese Journal of Physiology*—a journal available in few libraries in this country. Recent papers indicate that many authors are unaware of this diverse literature. This paper was prepared to draw together the early work, review Hou's papers, summarize the work that has appeared since, and present the results of recent experiments at the Delta Waterfowl Research Station.

EARLY OBSERVATIONS

Emperor Frederick II, in his monumental thirteenth century treatise on falconry (Wood and Fyfe, 1943:71), was seemingly the first to discuss the function of the oil gland of birds. He believed that its product not only oiled the plumage but also provided a poison which was introduced by the claws of hawks and owls thus bringing quicker death to their prey. In 1678 Willughby studied the question of the toxic nature of the oil gland secretion but found no evidence to support Frederick's contention.

The next mention of this gland was by Tyson in 1683. In his "Anatomy of the Mexico Musk-Hog" he pointed out the similar position of the scent gland in the musk-hog (=collared peccary, *Pecari angulatus*) and the uropygial gland in the partridge, and suggested that they were perhaps analogous. The possibility that this gland may serve a function in providing scent remains a moot question even today.

The chief reference to this gland during the next century seems to have been by the famed anatomist Cuvier in 1799 (Dallas, 1867:38-42), who provided the first description of the internal structure of the gland. He believed that it was a closed secreting vesicle but perhaps he examined a dove in which the gland is undeveloped and ductless for later workers have been able to trace and describe the ducts and, hence, it usually has not been considered an endocrine gland. From his study of the Gray Linnet (*Carduelis cannabina*), Monterosso (1915) believed it to function alternately as an endocrine gland and as a gland of external secretion; but details of his morphological studies alone seem to have reached publication.

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ANATOMY

During the nineteenth century and early in the twentieth there appeared a considerable number of thorough papers dealing with the anatomy of the oil gland, both gross and microscopic. Outstanding among those treating of the gross anatomy were Nitzsch (translation by Dallas, 1867), Owen (1866:230), Kossmann (1871), Paris (1910-13), and Granvik (1913).

The work of these men has shown that the uropygial glands are embedded beneath the skin in a mass of fatty tissue just dorsal to the levator muscle of the tail. The shape varies greatly among species and has considerable taxonomic significance (Coues, 1903:89). In various species the glands have from one to five openings (2-8, according to Grassé, 1950:285-289), to the outside through a nipple-like structure which is often covered by a tuft of specialized feathers. This tuft serves as a brush, functionally elongating the nipple and aiding in anointing the bill (Schumacher, 1919). At one time it was thought (Dallas, 1867) that the arrangement of these feather tufts was the best criterion for distinguishing some natural groups of birds both at the family and generic levels. The glands are best developed in aquatic birds. However, Burton (1822) pointed out that the oil gland is very small in Man-o'-war birds (*Fregata aquila*); when birds of this species were shot their plumage soaked quickly when they dropped into the sea. Gurney (1913:538-539) stated that the gland of the Gannet (*Sula bassana*) is the largest proportionally of all birds but is not used for lubrication of the feathers. Among parrots and doves are found all degrees of development of the gland from species with none to those with fully functional glands (Garrod, 1874a and b). It is absent in struthioniform, rheiform, and casuariiform birds and in some species of several other orders (Galliformes, Gruiformes, Caprimulgiformes, Apodiformes).

The gland is surrounded by a connective tissue capsule apparently devoid of muscle fibers (although Gadow, 1891:488, believed it to have a layer of smooth muscle) and receives its blood supply from the caudal artery; it is drained by the caudal vein which runs between the caudo-spinal muscle and the levator muscle. The nerve supply is from the first pair of caudo-spinal nerves plus additional sympathetic fibers. Kossmann (1871) electrically stimulated the nerve to one lobe of the gland and caused unilateral vasodilation of the artery to that lobe and a simultaneous flow of secretion from that lobe. Ligation of this artery stopped the flow. Paris (1906-13) confirmed these findings and added that the sympathetic nerve fibers must cause relaxation of the sphincter muscle around the external opening of the duct of the gland. This suggests many similarities to the sebaceous glands of mammals.

HISTOLOGY AND EMBRYOLOGY

The outstanding papers dealing with this aspect of the subject are those in

German (Kossmann, 1871; Granvik, 1913; Esther, 1938), French (Pilliet, 1889; Paris, 1912a and b), and Italian (Orlandi, 1902; Lunghetti, 1902-07; Monterosso, 1915). It is mainly from their works that the following summary has been drawn.

In the chick the gland appears first on the 9th to 10th days of incubation as a hollow invagination of the cutaneous epithelium in the rump region. Each lobe of the gland comes to have a stratified epithelium continuous with that of the duct of that lobe. Fat first appears in the gland cells on the 17th day of incubation (Ida, 1931).

The highly developed trabeculae of the inside of the gland resemble those of the heart of mammals and are packed with tiny parallel secretory tubules which produce their product by the gradual breakdown and sloughing of entire cells (a holocrine secretion, Biedermann, 1930; Grassé, 1950). The cell walls soon break down but leave the golgi apparatus intact in the secretion as revealed by special golgi stains (Bowen, 1926). Other cytological details and a discussion of the role of the mitochondria, golgi, and nucleus may be found in the work of de Jonge (1879), Röhmann (1902-04), Bowen (1926), and Hsu (1935, 1936). The weak reaction of the gland's secretion to osmic stains shows that there is little fat present in the product. This conclusion fits well with the histo-chemical work performed by Stern (1905a, 1905b). She concluded that the secretory, scarlet-red staining granules were present in the periphery of the tubules along with mitotic figures but increased in size toward the lumen while lipid granules with osmic acid affinity were scarcer toward the lumen and the fine fat granules were found throughout.

Smooth muscle fibers are found around each trabecula of the gland and also form a sphincter at the nipple of the excretory duct. It is probable that these muscles relax under the stimulus of the sympathetic nerve fibers, thus causing the gland to empty. Relaxation seems to be induced by contact of the bird's bill with the nipple of the gland, where the receptors of pressure sensation, the Corpuscles of Herbst, are clustered (Paris, 1912b; Schmidt, 1924).

PHYLOGENY AND HOMOLOGY

Students of comparative histology have been concerned with the probable homologies of the uropygial glands and have likened them to lizard skin or scent glands (Paris, 1913; Van Eggeling, 1931; Schmidt, 1924; Esther, 1938; to crocodile cloacal glands (Esther, 1938); to turtle tear glands and snake poison glands (Orlandi, 1902; Pilliet, 1889). However, Maurer (1895) saw no relationship to reptilian glands.

Many investigators have noted the similarity in structure of the uropygial glands of birds and the sebaceous glands of mammals (Kossmann, 1871; Furbringer, 1883; Joseph, 1891; Pilliet, 1889; Orlandi, 1902; Wigger, 1906; Paris, 1913; Biedermann, 1930). Kossmann (1871), Paris (1913), Pycraft

1910:15) believed that they serve the same function—that of true scent glands. In the sporting literature of that time it was frequently claimed that retrievers were able to find diving, crippled ducks by following the odor of the oil they left behind, and Herter (1929) maintained that leeches find their duck hosts in the same manner. It was suggested (Dallas, 1867) that the glands may serve as a repellent organ in such species as the Hoopoe (*Upupa epops*), for, in the incubating female, the secretion collects, turns black and gives off a powerful odor which persists as long as the young are in the nest. Ghidini (1906) and Coupin (1914) claim that the defense function of the gland in the nestlings of this species is extremely effective for the young store up the secretion until the nest is visited by some rodent or weasel whereupon they discharge the fetid fluid onto the intruder. A similar function is described by Hingston (1933) in the Great Hornbill (*Buceros bicornis*) where the yellow throat sites—the bill casque, neck, crown, rump and wing angles—receive their color from the oil of the uropygial gland.

The absence of uropygial glands in ratite birds led Beddard (1898:18–19) to conclude that glandlessness was a primitive character but Pycraft (1910:15) pointed out that anlagen of the glands were present in the embryo of some ratites and that the loss of the glands in the adult could be considered a secondary specialization rather than a primitive character.

GENETICS

The inheritance of glandlessness in doves was investigated by Johansson (1927) who found the condition to be recessive and frequent in the Fantail breed; it was not correlated with the number of tail feathers. Seven of 1,360 ordinary doves lacked the gland, which undoubtedly explains the disagreement between Darwin and Kossmann (Kossmann, 1871). More recently Kessel (1945) has reported on the inheritance of uropygial gland papillae in domestic fowl.

CHEMISTRY

Hou (1928b) states that the first analysis of the excretory product was made by Chevreul in 1853, who concluded that the sebaceous substance was developed by the setting free of a volatile acid in the presence of water. (This reference I have not been able to confirm for Hou's citation is in error). But a complete chemical investigation was not made until 1879, when de Jonge, in about two grams of the oil from a goose, found the following substances present: casein, albumin, nuclein, lecithin, low and high fatty acid, and a non-saponifiable portion, which he believed to be cetyl alcohol. Potassium, sodium, calcium, magnesium, and chlorine were found in combined form along with free sebacic acid and traces of sodium and potassium soaps. Newton (1893–96:653–654) reported that analysis of the secretion showed it possessed no sugar.

Röhmann (1904a) carefully repeated the chemical analysis and concluded that the secretion had only a small portion of fat (triglyceride of fatty acids) but a larger portion of fatty acid, ester of octadecylalcohol, and a chloroform-soluble body. Ida (1931) confirmed these findings. Röhmann (1902, 1904a) further pointed out that the gland must convert fat into fatty acids and then to wax—a hydrogenation through enzymatic action. He and de Jonge (1879) agreed that in 100 parts of the solid secretion approximately 60 are soluble in ether. The ether extract is a clear oil of yellow color which separates out as a nearly neutral, solid substance upon standing. It has an index of acidity of 0.75 to 3.4. The saponification index and iodine number are much less than for ordinary fat.

Although these early workers did not find cholesterol or the ester of cholesterol in the gland secretion of geese, Hou (1928b, 1930a) reported finding cholesterol in the glands and on the feathers of chickens. Ida (1931) found cholesterol in the whole gland but not in the secretion of the 17 species he studied. An earlier Japanese worker (Yamaguchi) whom Ida cites believed the gland excreted superfluous cholesterol.

In order to determine whether the uropygial glands actually synthesize the oil they secrete or merely convert dietary fats, Plato (1902) and Röhmann (1904a) fed geese on a diet of fat-free uncooked barley plus sesame oil and tested for the presence of the oil in the secretion of the uropygial gland at frequent intervals, determining that eight to 18 days are necessary for the transfer. However, it is not surprising that such an oil would appear in various fat depots of the body when the diet was overloaded with a foreign oil. More conclusive work was performed by Paris (1913) by feeding Sudan III in olive oil to ducks for several months. On autopsy peritoneal and body fats were stained orange but the oil of the gland was not. More controlled work was performed by Stern (1905a) by means of histochemical techniques in which she demonstrated that the outer zone of cells in the stratified epithelium actually contained fat droplets that were synthesized within the gland. Ida (1931) confirmed, in general, Stern's findings concerning the distribution of fat within the gland.

FUNCTION—ANECDOTES AND GENERAL OBSERVATIONS

In 1832 there began a prolonged argument over the supposed functions of the gland. This controversy raged in the pages of the *Magazine of Natural History* and was characterized by more heat than light. With much spirit and invective Waterton (1832, 1836, 1860) contended that birds' beaks were improperly shaped for such a purpose as dressing the feathers, that the feathers of the head and neck were as shiny as those of the body although not "preened" by the beak—"proof positive that the plumage of the bird has not

been lubricated with oil from the tail gland." He maintained that the sole function of the preening activities was removal of lice—which he claimed to have found in quantities in the gullets of birds he had skinned.

The Rev. Morris (1836) poked holes in Waterton's arguments and reported watching birds anoint their bills and crown feathers at the feather tuft on the oil gland. This was confirmed for ducks and pelicans by Crisp (1860), and Hussey (1860) gave a careful and cautious description of ducks' use of the bill in oiling their feathers. In the next year Matthews (1861) gave a convincing and detailed account of chickens observed at a distance of two feet immediately after a rain. The birds raised the feathers of the gland region, turned the head to one side, and squeezed the oil from the gland with their beak before wiping it off with the head and neck, which were in turn used to anoint the body plumage. This opinion was followed by Coues in the first and subsequent editions of his "Key to North American Birds" (1903:89).

Although Newton in his famous "A Dictionary of Birds" (1893:654) followed Coues' opinion, Pycraft (1910:15) sharply disagreed and suggested that, as in mammals, this gland served as a scent gland.

In 1910 Stubbs coined the term "feather-film" to describe the pile of cilia and barbules which keeps the surface film unbroken around the bird's plumage. He believed that the oil from the preen gland must play but a minor part for duck feathers which he washed in warm soda water and benzine retained their buoyant properties.

Here the sleeping dog lay until rudely awakened in 1929 by Eugene Law, who, upon reading the old controversy and little of the research of the intervening 70 years, made a valiant appeal for Waterton's case. Based on kitchen-table-type experiments he (1929) concluded that feathers carry no oil and that the sole function of the gland is to lubricate the beak (which is then polished on the feathers!).

The cudgels were again taken up by Madsen (1941), seemingly also unaware of the literature, who reiterated Law's contentions and cited his own simple experiments to show that ducks' feathers are waterproof strictly because their physical structure provides a hydrofuge mechanism. He believed that the tips of the belly feathers actually became wet so as to reduce friction in swimming!

Fabricius (1945) favors the opinion that the ability of the duck to keep its plumage dry is, at least in part, dependent upon the uropygial gland and that for normal functioning the diet of the downy young must include some substance provided by insects and crustaceans. However, thousands of normal ducklings have been reared at the Delta Research Station without these animals in their diet.

A similar role for the secretion of the oil gland and for powder down of birds has been suggested by Schüz (1927) and Esther (1938). Esther thought that powder in doves and other birds with powder down serves, in part, the same function as oil. Percy (1951:36-39) has provided photographic evidence of the concurrent use of powder and oil by the Bittern (*Botaurus stellaris*) and Heron (*Ardea cinerea*) after their plumage was contaminated by eel slime.

The early suggestion by Schauer (1877) that the gland had electrical properties was obviously a case of static electricity, discharged as his fingers touched the oil gland nipple in the dark of his laboratory.

OCLUSIONS AND ABLATIONS

Stoppage, both naturally and experimentally, and surgical removal of the oil gland provide some insight into its function.

A seven-inch "horn" protruding from the side of the uropygial gland of a Lapwing (*Vanellus vanellus*) was reported by Ticehurst (1910). This showed that stoppage and continued formation of the secretion resulted in rupture of the capsule and continuous oozing of the secretion, which came to solidify and harden. Similar excrescences were induced by Hou (1928b) by experimental occlusion of the gland.

Stoppage in chickens, resulting in enlargement, was found by Bechstein in 1791 (Hou, 1928b) and Crisp (1860). The former reported that it caused a disease known in France as "darre" while Coupin (1914) refers to it as "bouton." This seemed to be an old wives' tale until 1939 when Mohey reported a similar disease in cage birds and urban-dwelling chickens in India. He describes native as well as his own veterinary procedures for treating the disease.

Total removal of the gland by surgical procedure was first performed in Germany by Kossmann (1871), who saw no change in his pigeons following this treatment. The following year (1872) Philipeaux removed the uropygial gland from a duck and reported that the plumage remained normal, but the plumage of Hou's ducks (1928b) became dry and disorderly. Although these conflicting results perhaps are attributable to the small samples or poor operative technique, Philipeaux believed that when the ablation was performed on young ducks the gland was replaced by supplementary secretion in other skin glands in the region. But no one has found these "other skin glands." Joseph (1891) removed the glands from a few ducks and, after healing was complete, submerged them in water along with normal ducks. After a fifteen minute drying-off period the glandless birds retained in their plumage twice as much water by weight as did the normal birds.

The Italian histologist Lunghetti (1906) next performed ablations on a few 3-month-old chicks without apparent change.

Paris (1913) reported on the detailed structure of the uropygial glands of 350 different species of birds. His morphological work was accompanied by a few exploratory experiments. He ablated the glands in 10 birds (of 5 species) and saw no plumage changes. However, his birds were shunned by the controls. Coupin (1914) suggested that this might be due to their loss of normal body odor but a more convincing suggestion is that they might have been stealing some oil from the normal birds. This was actually seen by Hou (1928a, 1928b) when he ablated the glands in 16 pigeons, four chickens, four ducks and one goose. He then isolated the glandless birds from the controls and noted the following results:

1. By the fourth week, dulling and roughening of the plumage was seen with considerable soiling and very slow drying after bathing (ducks only?).
2. Heat loss, as shown by rectal temperatures before and after swimming in cold water, was greater in glandless birds than in controls.
3. Microscopic oil droplets normally present in great numbers on the barbs, barbules, and barbicels were progressively lost and completely disappeared by the third month, indicating that a bird normally removes oil as well as spreads it during preening and that in the absence of a new supply it eventually is entirely lost.
4. A slow, progressive decrease in body weight was noted, starting between 40 and 100 days after ablation of the oil glands.

Ida (1931) ablated the glands of ducks, chickens, and geese, finding no general changes in the plumage or appearance even when four months had elapsed. However, egg laying ceased.

Esther (1938) agrees with Paris and Ida in finding no general changes following gland ablation in his birds, which paired, bred, and reared several broods successfully when both sexes were made glandless. At the Delta Station one of the mallard hens, glandless for nearly a year, reared a brood successfully.

FEATHER STUDIES

Although Law (1929) made crude attempts to show that there was no oil on bird feathers and Madsen (1941) showed that feathers were wetttable with colored dyes, the only thorough work reported has been that of Hou (1928b). He took small bundles of feathers from control birds and birds from which the glands had been removed and, after drying these for 24 hours in a calcium chloride desiccator, subjected them to continuous fat extraction in an alcohol-

chloroform mixture in a Soxhlet's apparatus for 24 hours. The bundles were then removed, air dried, then desiccator dried and weighed. Those from control birds lost approximately 5 per cent in weight, while the feathers from glandless birds gained approximately 2 per cent. Although the weight gain remains unexplained, the substance removed from the feathers of control birds was, at least in part, cholesterol as shown by the Liebermann Burchard test. Cholesterol both from the feathers and the oil glands was further identified by spectrographic analysis.

Desiccator-dried feathers suspended in a saturated atmosphere gained moisture for 48 hours, and feathers from a saturated atmosphere lost weight in a dry atmosphere for 48 hours. This indicated that feathers are permeable to water. It was further shown that normal feathers subjected to an aqueous solution of methylene blue for an hour and then washed for two hours showed dye in the interior of the barbules.

Microscopic examination of feathers removed from birds several months after their glands had been ablated indicated that their loss of color and gloss was due to actual physical breakdown, undoubtedly in part the result of the preening activity itself. Seemingly, loss of the oil predisposed the feather to physical degeneration, making its wear more rapid, until it was possible to see, by microscopic examination, that there were actual holes in the feather due to breaking off of bits of the barbs.

It is of interest to note Hou's (1928b) observation that, after the feather is drawn through the blades of the beak, an act of swallowing invariably follows, indicating 1) that there is an automatic, instinctive behavior pattern, or 2) that something has actually been ingested. This might well be dirt, dandruff, lice, and oil. R. C. Murphy (1936:473-474) suggests that the stomach oil of procellariiform birds may be the secretion of the preen gland subsequently swallowed to be later regurgitated and used as a feather dressing. Fisher (1952:390-391) states that stomach oil is used in preening but clearly shows that this oil is produced in the proventriculus and not in the uropygial glands.

NUTRITION STUDIES

Hou (1928b) cites evidence that carnivores in zoos frequently develop rickets and may succumb on a diet of horse meat alone, while addition of intact birds or rabbits plus liver, fat, and flat bones prevents this. Rowan noted (1928) that his Merlins (*Falco columbarius*) needed feathers in their diet in order to remain healthy and that the mother forcibly fed these to her young every few days. Rowan suggested that the feathers might contain vitamin D resulting from irradiation by sunlight of oil spread on them from the preen gland.

A thorough study of the nutritional function of the preen gland product was reported in a series of papers by Hou (1928a, 1928b, 1929, 1930a, 1930b, 1931). A weak, rachitic pigeon in which the oil gland had been ablated was restored to health upon eating an irradiated gland from another bird. A second rachitic pigeon fed on a gland removed in the dark showed no improvement. Eight chicks (four of which were glandless) were placed on a rachitogenic diet until two died and all showed decalcification and swollen joints. Ultraviolet-light treatments which were then begun cured the controls of their rickets but not the glandless birds. The same results were obtained when the glands were removed in a group of four chicks after the rickets had developed—the controls again recovered under ultraviolet exposures but operated birds did not.

Adult pigeons, mallards, and chickens (kept in the sunshine after ablation of the glands) did not develop rickets but the plumage degeneration was severe. (The degenerative changes are never as severe in pigeons as they are in chickens and ducks.)

Guareschi's note (1934) suggesting a relationship between rickets, abnormal growth, and a keratinized uropygial gland in one chick and one pigeon added little to our knowledge.

Clark (1934) and Knowles, Hart, and Halpin (1935) removed the oil glands from three groups of Leghorn chicks at ten days of age. With nine birds in each group the first group was given a cod-liver oil supplement, the second ultraviolet treatments, and the third left on the rachitogenic base ration alone. Up to four weeks of age all gained weight like the normal unoperated controls but from this time on the third group developed rickets. Although they saw these results as a complete contradiction to Hou's work, it seems the conclusion should have been that rickets is easily prevented in the absence of the oil gland if therapy is started early, but, as Hou showed, once rickets has set in it is not readily cured by ultraviolet light. In brief, it is easier to prevent than to cure.

The last work of this sort reported was by E. F. Murphy (1936), who removed the oil glands and the combs from 50 Rhode Island Red chicks at the age of two weeks. One week later, along with an equal number of controls, they were put on a rachitogenic ration. The birds were treated as five groups, with ten glandless and ten intact birds in each group. There was a slight difference in the growth rates of the glandless and intact birds in the control group on basic ration alone, but apparently no significant difference in (1) the group receiving cod-liver oil supplement from the start, (2) the group given cod-liver oil starting with the fifth week, and (3) the group given 20 minutes daily irradiation after rachitic symptoms were apparent in the fifth week. But among the remaining group—those that received only five minutes of ultra-

violet irradiation from the start—the glandless birds were greatly retarded as compared with the intact birds. Analysis of the bones showed that in four of the five groups the intact birds had a slightly greater total ash content than did the glandless birds. Unaided by statistical analysis, Murphy concluded that there was no real difference in the responses of glandless and intact birds, but her data suggest to me that there may have been a real difference and that the thrift of glandless birds was much less than that of intact birds on a sub-minimal dose of ultraviolet light, although when given 20 minutes of treatment per day the thrift of glandless birds equalled that of intact birds.

This was shown earlier by Hou in his 1931 paper (again with too few birds) where he concluded that ultraviolet light cured rickets in chicks with or without oil glands when the legs and feet were exposed, quite regardless of whether the feathers were exposed or not. This later work was not in complete agreement with his first paper, and it seems clear that the threshold for ultraviolet therapy varies so much among species, and among breeds of one species, that consistent results cannot be expected when the irradiation is not measured and expressed in terms of actual dosage, as in the work of Maughan and Dye (1929).

Although we are forced to conclude that, at least in chickens, the presence of the preen gland is not essential for the prevention of rickets, it has not been shown that the gland does not play an important role. In another paper Hou (1930a) demonstrated that feathers contain vitamin D, that it can be extracted with fat solvents, and that the cholesterol content is twice as great in the feathers of intact birds as it is in feathers of glandless birds.

Hou tested thoroughly, by means of published roentgenograms taken at the start and at the end of the experiment, the effects of feeding feathers, feather extracts, and other parts of birds both normal and rachitic, to rats kept on a rachitogenic diet. The results are shown in Table 1.

TABLE 1
EFFECT OF FEEDING CHICKEN TISSUES TO RATS WITH RICKETS

Rachitogenic diet supplement	Per cent healing of rickets in rats fed on tissues from chickens	
	Normal	Glandless
Chicken feathers	70%	10%
Ether soluble extract of feathers	93%	0%
Skin	96%	38%
Body fat and muscle	90%	0%

This seems to be conclusive evidence that the oil on feathers of normal chickens contains an appreciable amount of vitamin D which could serve as a dietary supplement if accidentally ingested during preening. However, Ida (1931) found no cholesterol in the preen gland secretion, and Koch and Koch (1941) found no pro-vitamin D in alcohol-ether extracts of preen glands or feathers of ten-week old pullets when assayed on rats. The same procedures demonstrated that extracts from skin and legs of the pullets did cure rickets in rats.

Some of the seeming contradictions in these experimental results may be due to the difference in age of the birds from which feathers were clipped for chemical extraction and tests for vitamin D. Hou (1930a) pointed out the significant difference in the ability of young and adult chickens to store anti-rachitic factor. Adult birds kept in the dark on a rachitic diet for four months after the oil glands were removed retained in their skin and fat appreciable amounts of anti-rachitic factor, while young kept in the sunlight for four months following ablation of their glands completely lost this factor.

RELATIONSHIP OF OIL GLAND TO ENDOCRINE GLANDS

Ida (1931) found that not only were no more eggs layed by the ducks, geese, and chickens from which he had removed the uropygial glands but that from 146 to 204 days after operation there was complete atrophy of the gonads in both sexes. This has not been found by any of the later workers.

Esther (1938) suggested that the uropygial glands of doves had some endocrine relationship for he found that the inner epithelial lining of the gland developed rapidly in nestlings after hatching but atrophied as soon as the young no longer received pigeon milk. A much earlier suggestion was made by Mac-Gillivray (1837:44-45) that the function of the gland was related to the molting process for he found it highly developed during molt and greatly diminished after the molt was complete. This lead seems never to have been investigated further. Grassé (1950:285-289) states that the gland seems better developed in the male than in the female and that in the goose it reaches maximum size in January and February.

That the size and amount of secretion of the uropygial glands is under the influence of sex hormones was first suggested by Selye (1943) when he stated categorically: "It is known that during the mating season it [the uropygial gland] produces an increased amount of secretion at least in certain species." He injected Leghorn chicks, starting on the second day of life, with various steroid hormones, and found that testoid hormones depressed the uropygial glands between the 20th and 45th days but that the glands then resumed normal size and histology in spite of continued hormone treatment.

Kar (1947) found that the uropygial glands of Leghorn cockerels atrophied as a result of castration in 36 days from an average weight of 604 mg. to that of 345 mg. This atrophy was prevented by injections of the male hormone, testosterone. The same male hormone depressed the weights of uropygial glands in normal chicks but female hormone (diethylstilbesterol) did not. In old capons (age 156 days) the gland had returned to normal size without hormone injections, probably due to male hormone supplied by hypertrophy of adrenal cortical tissue.

These findings all suggest that the amount of uropygial gland secretion is under the influence of male sex hormone.

EXPERIMENTS AT DELTA, MANITOBA

Preliminary experiments concerning the function of the uropygial glands of ducks were made at the Delta Waterfowl Research Station at Delta, Manitoba, in the summer of 1947. Glands were surgically removed from 5 Redhead (*Aythya americana*) and 5 Shoveller (*Spatula clypeata*) ducklings less than ten days of age. All were kept in the hatchery where healing was observed to be prompt. The ducklings were normal in appearance and behavior until the juvenal plumage was assumed in August. The rough and dull look of the feathers was apparent at the time the birds were released on a large outdoor pond. They seemed to swim and dive normally but quickly became wet and bedraggled. Survivors were kept over winter in the hatchery but did not do well—their soiled, dry, roughened plumage was definitely inferior to that of normal ducks kept with them.

Early in July, 1951, glands were removed from 9 Mallards (*Anas platyrhynchos*) and 23 Redheads in order to study growth and survival in comparison with controls of the same age. Observations were also made of behavior and plumage changes induced by ablation of the glands. Because Hou (1928a, 1928b) saw evidence of glandless birds attempting to steal oil from normal birds, our controls were kept in separate pens from the operated birds without glands.

Preening Behavior. In the Redhead ducklings the preening behavior pattern was observed repeatedly both in glandless and intact birds. No alteration in the act either in sequence or frequency of occurrence could be detected in the birds deprived of their oil glands. They were seemingly unaware of the futility of their movements; the whole behavior pattern is probably innate, although it becomes more elaborate as the number of feathers to be preened increases with age.

Although the details are difficult to observe, the sequence of events is usually as follows: The tip of the bill is touched to the area of the gland's

nipple. Slight nuzzling movements suggest that the tactile-sensitive Corpuscles of Herbst are being stimulated. It is possible that the nipple is actually squeezed between the mandibles but this could not be observed for certain. (Manual manipulation by the observer did not elicit flow of the gland's secretion.) Apparently the stimulation from the duck's bill induces flow of the gland's secretion and immediately afterward the lower mandible, chin, sides of head, and occasionally the top of the head are wiped across the nipple. The lower mandible is then rubbed over the breast and belly feathers. Some feather arrangement may be accomplished at the same time. Use of the bill in preening feathers in other regions seems to be primarily a matter of feather arrangement and is usually accomplished without prior application to the oil gland.

The remainder of the body plumage, namely the flanks, back, and scapulars, is treated by being rubbed with the sides of the head and chin. The flight feathers are rarely touched with the bill but may receive oil when the sides of the head are rubbed along the sides of the body.

The pattern of the preening behavior is usually as described above although the sequence of events may vary. Frequent preening was observed during which, and prior to which, no use was made of the oil gland. Such feather arranging is probably much more frequent than is preening following use of the oil gland. The complete preening pattern, including the movements attributed to anointing the head and bill in the normal birds, was observed in both intact and glandless ducklings up to the age of seven weeks, when the summer's study period ended. The preening pattern is seemingly innate for it persisted in these glandless ducks and was repeatedly seen during the following summer after the birds were fully adult.

Most of the same preening behavior described for the Redhead was also seen in Mallards although the condition of their housing made them difficult to observe.

At the age of five weeks one of the groups of glandless Redheads was placed in the same pen with a group of normal ducklings in order to watch their reactions to each other. At no time during the ensuing two weeks were glandless birds seen to attempt to steal oil from their intact companions as was described by Hou (1928b), nor was stealing seen the following summer when the ducks were adult.

Plumage Comparison and Behavior toward Water. The difference in appearance between glandless and normal ducks, especially in the Redheads, was striking. The feathers of normal birds were glossy and kept well arranged while those of glandless birds were dry, lusterless, and matted (see Figs. 1 and 2). The difference was even more apparent when the birds emerged from water; feathers of the normal ducks remained dry, glossy and in place, while

those of the glandless ducks became completely water soaked, matted, and disarranged.

Although there was some variation in the behavior of different pens of Redheads under observation so far as their use of water was concerned, it was obvious that glandless birds avoided water even to the extent of being cautious

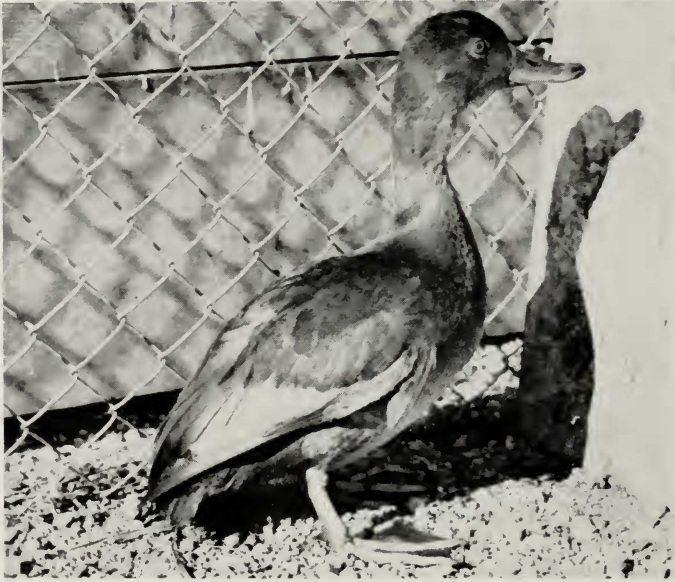


FIG. 1. Normal, hatchery-reared Redhead, age approximately 15 weeks.

about slipping down the incline of the pens during feeding. In contrast, the normal Redheads, by seven weeks of age, spent much of their time on the water—feeding, playing, and preening—and even rested on the water at night. The difference in the condition of the plumage in normal and glandless birds seems to be an obvious explanation for the disparity in amount of use made of water by the two groups.

Differences in plumage of intact and glandless birds disappeared with the completion of the molt the following summer. The glandless birds were not only restored in appearance but also in behavior for they no longer avoided the water but swam and bathed with other ducks on the pond. The glandless ducks had to be caught and the leg band numbers read in order to distinguish them from normal birds. However, their plumage again showed deterioration during the ensuing winter and was again fully restored to normal by molt in the next summer (their third year of life). Madsen (1941) reports that one

adult duck from which the gland was removed just prior to molt was normal in appearance and behavior after the molt was completed. Heinroth (1928, 1:32-33) mentioned that sea ducks which have lost their water-proofness as a result of being shipped in a basket are restored to normal at the next molt, if they survive that long.



FIG. 2. Hatchery-reared Redhead, 15 weeks of age, from which oil gland was removed during first week of life.

Skin and Bill Condition. In the glandless ducks the surface of the bills, legs, and feet became dry; the bill peeled, the skin of the legs and feet thickened and cracked. This condition, especially of the legs and feet, was extreme by the following summer, after the glandless birds were more than one year old. It persisted after the birds were turned out on the enclosure pond and lived under natural conditions. Although the glandless birds' plumage was restored to normal after the eclipse molt, the skin condition did not improve. This reminds one of the suggestion first made by Trouessart (1906) that the oil gland was essential for oiling the skin as well as the feathers. In their third summer the glandless ducks at the Delta Station had completely normal plumage, bills, and legs after the molt.

Growth and Survival. In order to determine what effect removal of the oil glands might have on the growth of ducklings, both glandless and normal birds were weighed at frequent intervals. The average weights for each group

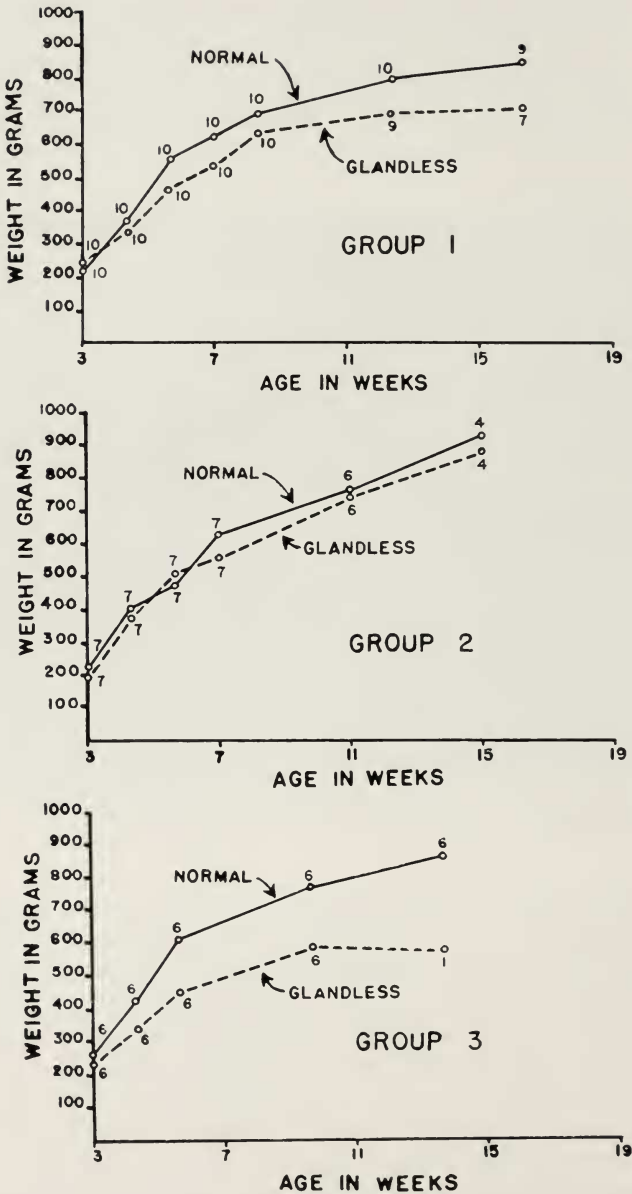


FIG. 3. Growth rates of 3 groups of Redheads in the Delta hatchery. The numbers of birds alive at each weighing are shown by the figure adjacent to each point on the curves.

of Redheads and Mallards throughout the summer growth period are shown in Figs. 3 and 4. It may be seen from examination of these figures that in

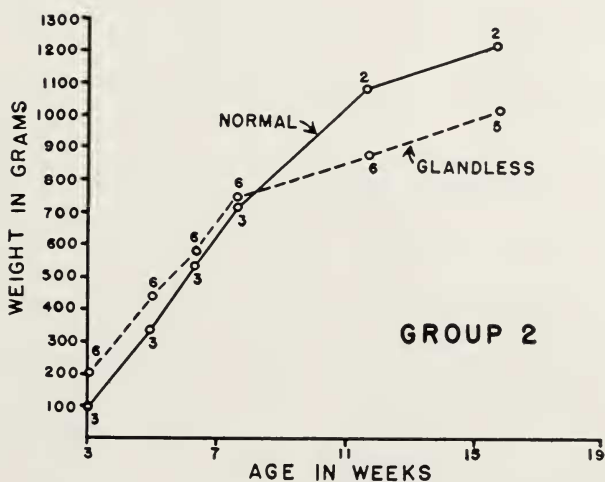
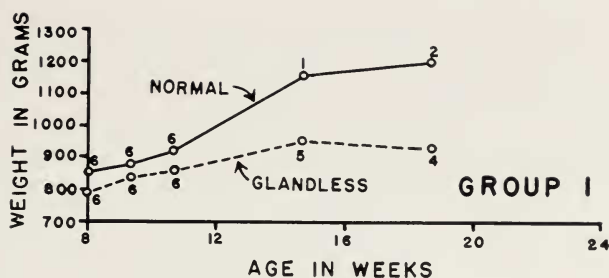


FIG. 4. Growth rates of 2 groups of Mallards in the Delta hatchery. The numbers of birds alive at each weighing are shown by the figure adjacent to each point on the curves.

each of the five groups of ducks the normal, intact birds showed a more rapid gain in body weight than did the corresponding group of birds from which the oil glands had been removed.

It seems certain that the oil gland is essential for maintenance of maximum thrift in ducks and that the differential growth rates shown by intact birds in captivity would be even greater in the wild. Although it is possible that the intact birds gained faster because of vitamin D supplement received through preening, it seems more likely that the difference in the two groups may be mainly attributed to the more efficient insulating layer provided by the feathers of the normal bird. The heat loss suffered by the glandless birds with matted plumage must be a constant drain depriving the birds of energy otherwise used for growth. It is doubtful that glandless ducks could long survive in the wild. Among the Mallards held in captivity, three of the 12 glandless birds

died by February but all of the normal birds were still alive. Among the Redheads 13 of the 23 normal birds died by February and 17 of the 22 glandless birds succumbed during the same period.

Species Differences in Size of Oil Gland in Proportion to Body Weight. Crisp in 1860 was first to show interest in the general relationship of preen gland weight to body weight and gave examples from several species. Because the size of the oil glands of water birds has frequently been pointed out as exceeding that of land birds, it might be anticipated that the glands of diving ducks would be larger in proportion to the body weight than would be those of dabbling ducks. As one test of this, all glands removed from young ducklings were weighed and compared with the weights of the birds from which the glands had come. The results were as follows:

Species	Number of birds	Per cent of body weight made up by oil glands
Redhead	24	0.54
Mallard	12	0.31
Shoveller	5	0.40

Glands from more species and from older birds would be required before correlations should be made.

Buoyancy and Wetting Time in Incubator-Hatched Ducklings Compared with Wild-Hatched Ducklings. Madsen (1941) claimed that in Eider duck nestlings (*Somateria mollissima*) the oil glands do not become functional until several days after hatching, but that these young have no difficulty remaining dry while swimming. It may be possible that young ducks are copiously anointed by their mother before leaving the nest (Heinroth, 1911) or that the downy young get enough oil from contact with their mother's feathers (Heinroth and Heinroth, 1928, 3:211-212) to make them water-repellent until their own glands become functional.

As one test of this hypothesis, four downy young of approximately three days of age were taken from a hen Redhead that chanced to pass the Delta Station with her brood. The behavior of these birds was studied in comparison with four downy young Redheads of the same size that had been hatched in the incubator. The birds were tested singly and as a group by placing them in washtubs half filled with ordinary water for 15-minute observation periods.

Wild-hatched ducklings seemed to float a little higher in the water, were more at ease, less active, never jumped in attempts to escape, and did not get wet. Incubator-hatched young began jumping to escape within 8 to 10 minutes

and showed more wetting of the outer belly down. The basic question remains unanswered: Did these ducklings jump to escape because they were getting wet or did they get wet because they were jumping?

A further test of the two groups of young was made the following day by placing each bird alone in a tub containing 25 liters of water to which had been added 50 grams of the wetting agent "Alconax." With wild-hatched Redheads jumping now began in $\frac{1}{2}$ to 1 minute and within $3\frac{1}{2}$ minutes all sank until only the head remained above the surface. Each was then quickly rescued, dried and later used for another trial on a later day. There was no progressive decrease in wetting time during the four trials as might have been expected had an oil film been removed by the concentrated solution of "Alconax." With the four incubator-hatched Redheads jumping began earlier and sinking to the level of the head occurred in half the time required by wild-hatched young. Again the cause of the earlier jumping could not be ascertained.

Application of a cigarette paper to the feather tuft on the oil gland of newly hatched ducklings from the incubator at the Delta Research Station always produced a greasy spot, indicating that the gland was functional in the first day of life in the Redhead, Canvasback (*Aythya valisineria*), and Mallard. This is in agreement with Esther (1938) who found the gland functional in the first day in domestic ducks and the Coot (*Fulica atra*). However, neither Madsen (1941) working with the Eider duck nor Veselovsky (1951) working with the Tufted Duck (*Aythya fuligula*) believed the gland to be functional in the first few days of life.

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CONCLUSIONS CONCERNING FUNCTION OF THE OIL GLAND

From the welter of opinions, inconclusive observations, and contradictory experimental evidence reported in the literature, plus observations made at the Delta Waterfowl Research Station, the following general conclusions concerning the functions of the uropygial glands of birds seem justified.

1. The oil gland of birds secretes a substance containing much fatty acid plus some fat and wax. The act of preening induces, through a nervous re-

flex, flow of the secretion onto the nipple or feathers occurring at its opening. This substance is transferred to the body plumage and probably also to the wing plumage by the bill and head plumage.

2. In waterfowl the secretion of the oil gland maintains the water-repellent quality of feathers either directly or by preserving their physical structure.

3. In waterfowl the secretion is essential for maintenance of feather structure from one molt to the next. Without this secretion the feathers lose much of their normal function both as a flight mechanism and as a heat-insulating medium. It seems unlikely that a bird rendered glandless could survive in the wild.

4. Degenerative plumage changes following removal of the glands are more pronounced in waterfowl than in chickens and more pronounced in chickens than in pigeons. This seems reasonable in view of the general relationship of gland size and probable need for "waterproofing."

5. The degenerated plumage of Mallards and Redheads caused by removal of the glands when the birds were in the downy young stage is lost through normal molt during the following summer and the new plumage is normal in appearance, at least at first.

6. The secretion is used to anoint the bill and maintains its surface structure and glossy appearance; without the secretion the bill becomes dry and shows some sloughing. Neither the bill condition nor the dryness and cracking of the skin of the legs of glandless birds improves during the molt in the second summer of life but in the third summer their appearance is normal in every respect after the molt.

7. The rôle of the uropygial gland as a scent gland remains a complete enigma.

8. The uropygial gland is not essential for growth and development but in its absence growth is impaired in Mallard and Redhead ducks.

9. Hou's papers (1928-1931) seemed to show that the feathers of normal intact chickens (probably adult) contain vitamin D which is lacking in the feathers of glandless chickens and that these feathers have twice the cholesterol content of feathers from chickens having had their glands previously removed. These findings could not be confirmed by later workers (Koch and Koch, 1941) using pullets.

10. Although growth of glandless birds was slower than growth of intact Mallards and Redheads, the secretion of the gland can not be considered essential in the diet; however, if it is ingested in even small amounts following the act of preening, the vitamin D it is said to contain may significantly augment in the growing bird the usual dietary supply of that vitamin.

11. The preen gland is not essential for the maintenance of life in the laboratory; it certainly is essential for survival in the wild.

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